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THE EVOLUTIONARY SIGNIFICANCE OF ROTATION OF THE OÖTHECA IN THE BLATTARIA

By Louis M. Roth

Pioneering Research Division

U.S. Army Natick Laboratories, Natick, Mass.

The newly-formed oötheca of all cockroaches projects from the female in a vertical position, with the keel and micropylar ends of the eggs dorsally oriented. All of the Blattoidea (Fig. 1) and some of the Blaberoidea carry the egg case without changing this position. However, in some of the Polyphagidae (Figs. 11-16) and Blattellidae (Figs. 2,3), and all of the Blaberidae, the female rotates the oötheca 90° so that the keel faces laterally at the time it is deposited on a substrate (Polyphagidae, Blattellidae), carried for the entire embryogenetic period (*Blattella* spp.), or retracted into the uterus (all Blaberidae). According to McKittrick (1964), rotation of the oötheca frees the keel from the valve bases which block an anterior movement of the oötheca while it is in a vertical position, and it orients the oötheca so that its height lies in the plane of the cockroach's width, thus making it possible to move the egg case anteriorly beyond the valve. It is likely that by the time the oötheca had evolved to the stage where it was retracted internally, the height of the keel had been greatly reduced (e.g., in *Blattella* spp.) and it would not be necessary to free its keel from the valve bases. The eggs of Blaberidae increase greatly in size in the uterus during embryogenesis (Roth and Willis, 1955a, 1955b). A logical advantage for rotating the oötheca prior to retraction resulted in orienting the eggs in the female's body in a position which would permit the uterus to increase in size as the embryos developed. When stretched by a newly deposited oötheca, the uterus of a blaberid presses against the inner surfaces of the tergum and sternum but there is lateral room for expansion. If the oötheca was not rotated prior to retraction, the long axes of the eggs would lie vertically and during gestation the uterus would have to stretch dorso-ventrally, a direction which allows little room for expansion in these relatively flat insects.

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Hebard (1919) described a specimen of *Lissoblatta flabellata* (Saussure) which was carrying a partially extruded oötheca in a horizontal position, and another female of the same species with an oötheca that was slightly less extruded than the above specimen but with the suture dorsad. Hebard concluded that "The position in which the oötheca is carried would, from this evidence, again appear to have little or no significance in systematic work in the Blattidae." Unfortunately, this conclusion was based on how the oötheca happened to be carried when the female was collected and preserved. This is also true of Karny's (1924) and Bey-Bienko's (1950) observations that the oötheca of *Ectobius* is carried with the keel upright; prior to its deposition the oötheca is rotated in species of this genus (Brown, 1952; Roth and Willis, 1957).

The manner in which the oötheca is carried while it is being formed is unimportant taxonomically since it is the same in all cockroaches. How the egg case is carried at the time it is being deposited is significant taxonomically and important for understanding the evolution of ovoviviparity and viviparity. Dried museum specimens cannot always be used to determine whether or not rotation of the oötheca takes place. If, in a museum specimen, the oötheca is carried vertically in the vestibulum, it does not necessarily mean that this is its position when it is deposited. The danger of using museum specimens in determining rotation was emphasized when I examined specimens in the Rehn and Hebard collection at The Academy of Natural Sciences of Philadelphia. A specimen of *Cariblatta minima* Hebard had the oötheca oriented with the keel laterad. This may have been the specimen which Hebard (1917) used in claiming that *C. minima* rotated its egg case. It was apparent that the egg case had been glued on the female, and in doing so it was reoriented when inserted into the female's vestibulum. Roth and Willis (1954) found, by observing living females, that the oötheca of *Cariblatta* is not rotated prior to

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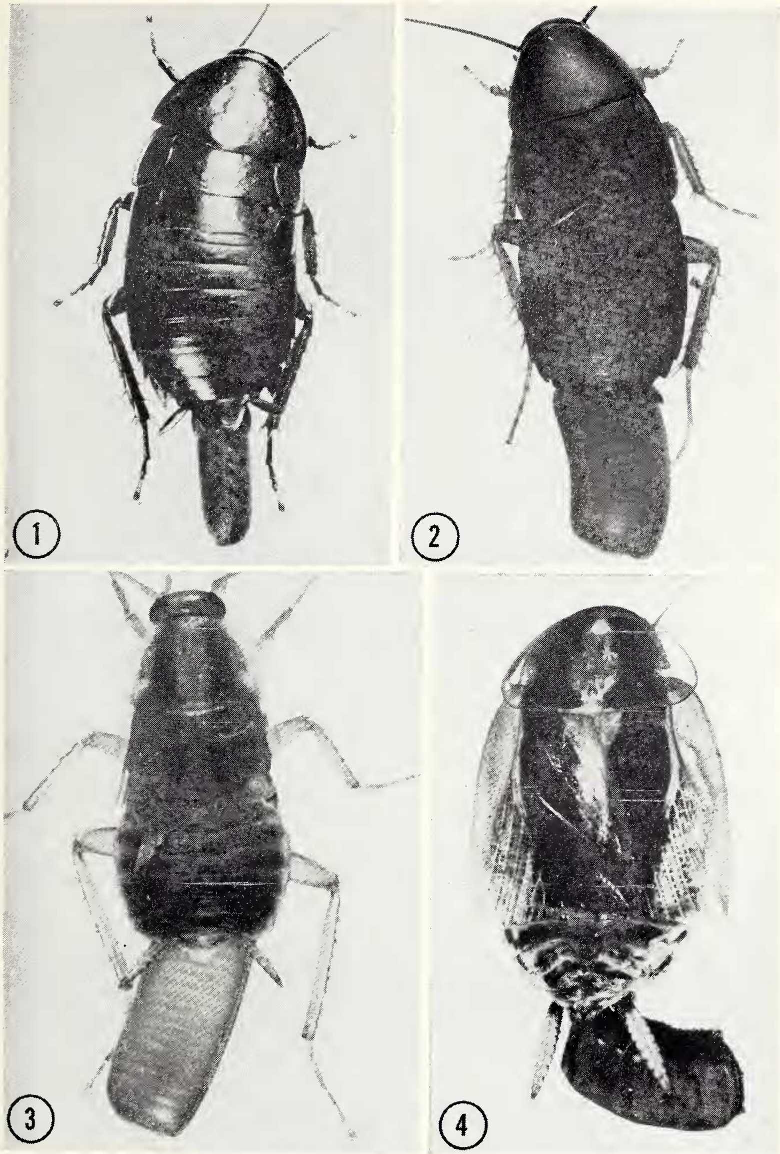
Explanation of Plate 15

Figures 1-4. Females of Blattaria carrying oöthecae. Fig. 1. *Maoriblatta novae-seelandiae* (Brunner) (Blattidae) (formerly *Platyzosteria novae-seelandiae* Brunner; Princis, 1966). No rotation, (× 2.0). Fig. 2. *Ischnoptera deropeltiformis* (Blattellidae: Blattellinae). Advanced rotation, (× 3.6). Fig. 3. *Blattella germanica* (Blattellidae: Blattellinae). Advanced rotation, (*ca* × 4.9). Fig. 4. *Dendroblatta sobrina* (Blattellidae: Plectopterinae). Aberrant "rotation" resulting from the female having difficulty in depositing the oötheca. This species does not normally rotate its oötheca. (× 5.7)

(Figs. 1 and 2 from Roth and Willis, 1960)



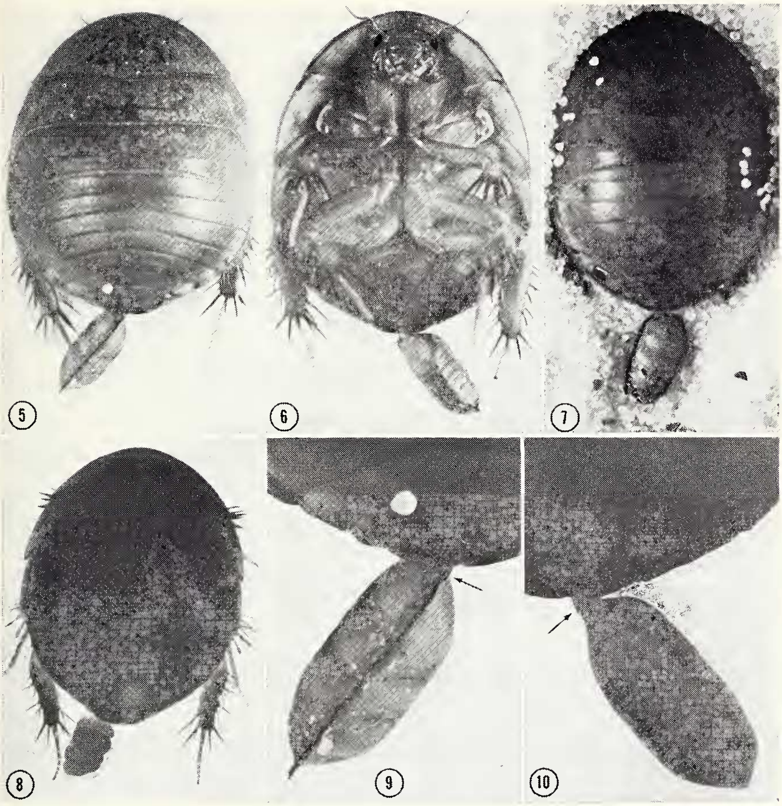
Roth — Blattaria

deposition. At the Academy, I also saw pinned specimens of *Dendroblatta sobrina* Rehn (Plectopterinae), *Chorisoneura barticae* Hebard (Plectopterinae), and *Periplaneta brunnea* Burmeister (Blattinae), each bearing an oötheca with the keels facing laterad. These genera do not normally rotate their oöthecae (see below). In the *Chorisoneura* female the abdomen was obviously abnormally flattened and the oötheca must have been "rotated" artificially when this occurred.

Rotation of the oötheca is an important behavioral taxonomic character in the Blattellidae and may be used to separate the nonrotators (Anaplectinae and Plectopterinae) from the rotators (Blattellinae, Ectobiinae, and Nyctiborinae) (McKittrick, 1964). The absence of rotation led to a study which resulted in the erection of 2 new genera, *Agmoblatta* and *Isoldaia,* of Plectopterinae; these were formerly Blattellinae, in the genus *Loboptera* (Gurney and Roth, 1966). According to Hebard (1919) *Lissoblatta flabellata* rotates its oötheca. Princis (personal communication) claims that *Lissoblatta* is a synonym of *Riatia.* McKittrick (1964) placed *Riatia* in the nonrotating Plectopterinae. Hebard may have erred in his interpretation of the position in which the oötheca was carried, or the generic placement of this genus requires additional study.

I place the following species, whose genera are included in the Blattellidae (Princis, 1960) in the Plectopterinae because the females do not rotate their oöthecae: *Dendroblatta sobrina, Ellipsidion affine* Hebard, *Euphyllodromia angustata* (Latreille), *Latiblattella* sp. nov. I would also place *Celeriblattina* Johns in this subfamily because, according to Johns (personal communication), it does not rotate its oötheca. The following Blattellidae (Princis, 1960) rotate their oöthecae and I include them in the Blattellinae: *Chorisia fulvotestacea* Princis, *Gislenia australica* (Brunner), *Ischnoptera rufa rufa* (Degeer), *I. panamae* Hebard, *I. deropeltiformis* (Brunner), and *Nesomylacris relica* Rehn and Hebard; the following have been reported to rotate their oöthecae and are therefore included in the Blattellinae: *Loboptera decipiens (Germar)* (Lefeuvre, 1959, Gurney and Roth, 1966), *Lobopterella dimidiatipes* (Bolívar) (McKittrick, 1964, as *Loboptera;* Princis (1957) used *Loboptera dimidiatipes* to erect *Lobopterella*), *Tartaroblatta* Bey-Bienko (Bey-Bienko, 1950), *Ignabolivaria* Chopard (Bey-Bienko, 1950), *Aristiger histrio* (Burmeister) (Karny, 1924, as *Hemithyrsocera histrio;* Princis (personal communication) says that this species is now *Aristiger histrio*), and *Parellipsidion* Johns (Johns, 1966).

I have seen very few instances of "rotation" in Plectopterinae. One female of *Dendroblatta sobrina* (Fig. 4) and 2 females of *Lopho-*



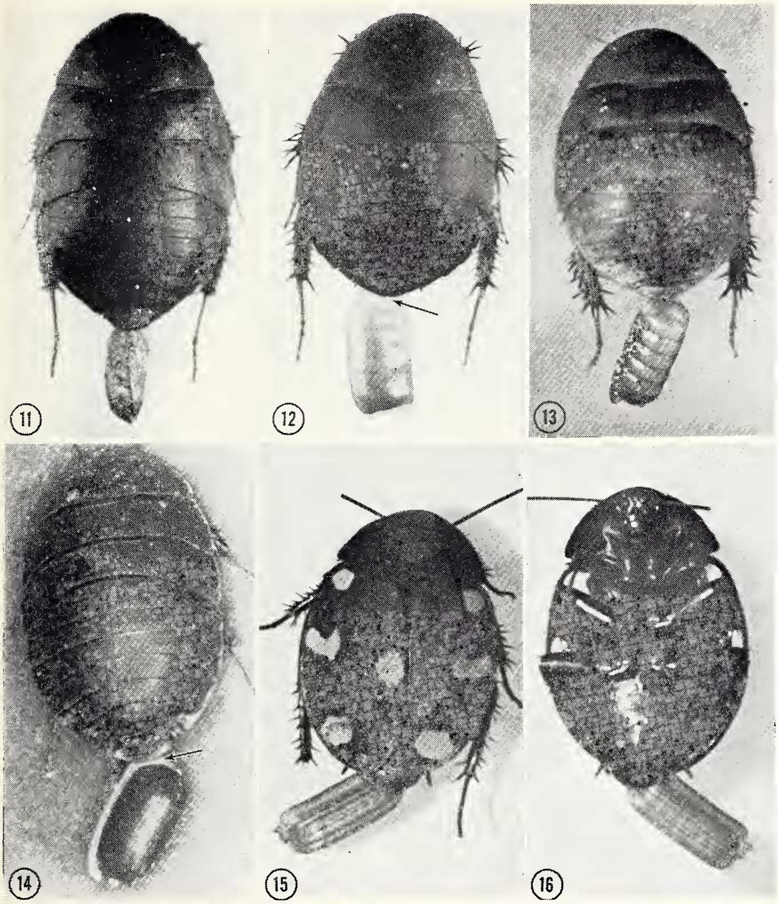
Figures 5-10. *Arenivaga (Psammoblatta) cerverae* carrying a completely formed oötheca. Fig. 5. Dorsal view, (× 2.1). Fig. 6. Ventral view, (× 2.1). Fig. 7. Dorsal view of a female in sand; the oötheca is twisted so that the keel faces to the left, (× 2.2). Fig. 8. Dorsal view; light coming from below showing the eggs visible inside the oötheca. Note that the anterior eggs do not lie in the vestibulum, (× 1.9). Figs. 9-10. Enlarged views of the oötheca shown in figures 1 and 2; note the flange (arrows) held securely in a vertical position by the paraprocts. (× 5.3)

blatta sp. nov. rotated their oöthecae but these were instances in which the females apparently had difficulty in dropping the egg cases.

I have observed many females of the desert polyphagid, *Arenivaga (Psammoblatta) cerverae* (Bolívar) oviposit. Sometimes the oötheca was oriented with the keel laterad (Figs. 7,8) but this was not because they had been rotated. The oötheca of *A. cerverae* has a long flange (Figs. 17,19) or "handle" which is held vertically between the parapracts (i.e., the flat surface of the flange is in a vertical plane) (Figs. 9,10). When the female is on a sandy substrate, she tends to sink into the sand particles, and because the flexible flange is twisted, the oötheca may be held with the keel laterad (Fig. 7). If the female is raised off the substrate the oötheca hangs in its normal position with the suture dorsad (Figs. 5,6).

Although Alfieri (1921) briefly described and illustrated the oötheca of *Polyphaga aegyptiaca* (Linnaeus), he did not mention whether or not it was rotated prior to its deposition. At the Philadelphia Academy I saw a female specimen of *P. aegyptiaca* with an oötheca on the same pin. The collection data stated "Alive and bearing oötheca horizontally in raw opium from Smyrna, Asia Minor. At Quarantine Port of New York — VII-3-1919, H. B. Shaw." In our laboratory culture I have seen females of *P. aegyptiaca* carrying oöthecae more than a dozen times. In only 3 instances were the egg cases carried with the keel laterad and this was apparently not normal. The oötheca of *P. aegyptiaca* also has a flange (cf. Figs. 17 and 18) by which it is held in the paraprocts. However, the flange is relatively shorter and more rigid than that found in *A. cerverae*. The supra anal plate of the female of *P. aegyptiaca* has a median cleft in it, and the very high keel (Fig. 18) of the extruded egg case lies between the margins of this indentation; this helps to support the oötheca in a vertical position. When the female is jostled by other individuals in the culture, or for other reasons, the keel may be disengaged from the cleft of the supra anal plate. Because the oötheca is not firmly inserted but is held by a flange between soft paraprocts, the large egg case may fall on its side. When in this position, one can be misled into thinking that rotation has occurred. The twisted oötheca can be turned upright easily without disengaging it from the female indicating the flexible nature of how it is held. The oötheca of *Polyphaga saussurei* (Dohrn) and *P. indica* Walker have flanges (Bey-Bienko, 1950) somewhat similar to that of *P. aegyptiaca*. The egg case of *Euthyrrapha pacifica* (Coquebert) (Fig. 20) also has an elongated flange which is probably flexible, but nothing is known about the oviposition behavior of this species.

In the polyphagids, *Arenivaga (Arenivaga)* spp. (Figs. 11-13), the female rotates the oötheca in a manner similar to that figured by McKittrick (1964) in *Arenivaga (Arenivaga) bolliana* (Saussure) (Fig. 14). However, McKittrick (1964) did not consider this to be rotation because once rotated, the oötheca is attached to the female only by a flange (Figs. 12,14 arrows) and none of the eggs are hidden within the vestibule (McKittrick, personal communication).



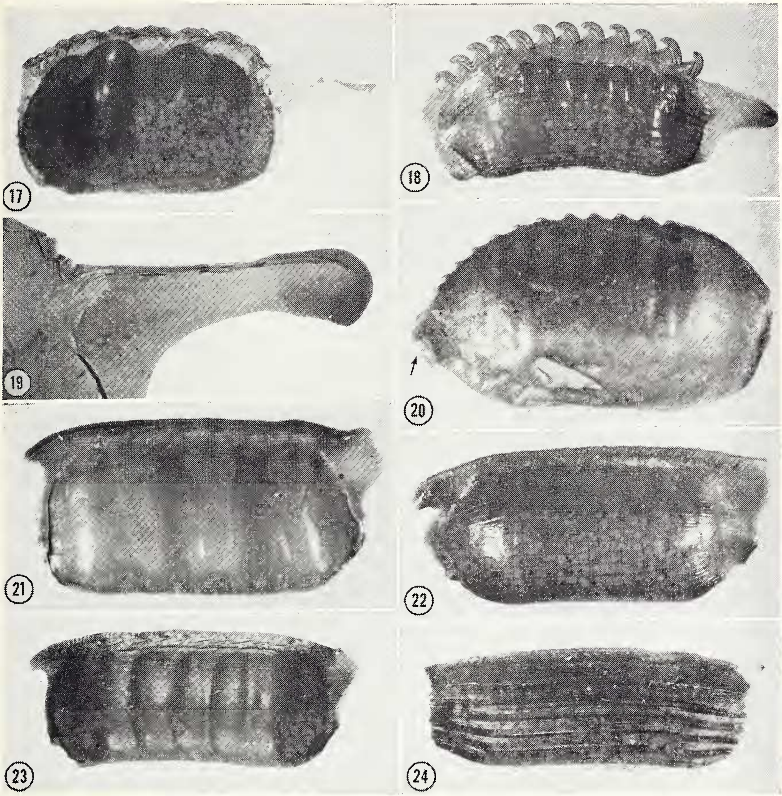
Figures 11-16. Primitive rotation of the oötheca in the Polyphagidae. Figs. 11-12. *Arenivaga (Arenivaga)* sp. *A* (Kelso Dunes, California). Fig. 11. Oötheca being formed and still in the vertical position. Fig. 12. Oötheca rotated with keel to right, (× 2.8). Fig. 13. *Arenivaga (Arenivaga)* sp. *B* (Coachella Valley, California). Oötheca rotated with keel toward left. Note the flange by which the oötheca is held and that none of the eggs are hidden in the vestibulum, (× 2.0). Fig. 14. *Arenivaga (Arenivaga) bolliana.* Oötheca rotated toward left. (From McKittrick, 1964; courtesy of Dr. F. A. McKittrick), (*ca.* × 1.9). Figs. 15-16. *Therea petiveriana* (India). Oötheca rotated to left. 15. Dorsal view. 16. Ventral view, (× 1.6).

(Arrows in Figs. 12 and 14 point to flange by which the oötheca is held between the paraprocts).

The flanges of the oöthecae of the subgenus *Arenivaga* (Figs. 21-23) are considerably shorter than the flanges of the subgenus *Psammoblatta* (Figs. 17,19) or of *Polyphaga aegyptiaca* (Fig. 18), and suggest that within the Polyphagidae there has been a reduction in the length of the flange. According to McKittrick (1964) the oöthecae of some of the more primitive Plectopterinae still have a flange.

Since rotation is defined as a reorientation or turning of the oötheca 90° so that the keel faces laterally, I consider the manner in which *Arenivaga (Arenivaga)* spp. carry their egg cases prior to depositing them, as true rotation. However, this may be considered to be a primitive type of rotation because none of the eggs are enclosed or hidden within the vestibulum of the female after the egg case is turned 90°. The polyphagid *Therea petiveriana* (Linnaeus) also rotates its oötheca (Figs. 15,16) prior to depositing it, as figured by Ananthasubramanian and Ananthakrishnan (1959). Because of the supra-anal plate, it appears as though some of the anterior eggs are within the vestibulum of the female (Fig. 15). However, when viewed ventrally (Fig. 16) one can see that none of the eggs are hidden inside the female. The flattened upper anterior corner of the oötheca (Fig. 24) is the only part held by the female. McKittrick (1964) claims that the polyphagid *Hypercompsa fieberi* (Brunner) does not rotate its oötheca. However, she (personal communication) based this conclusion on a preserved female that was carrying a fully formed oötheca with the keel upright. This female may have been preserved prior to rotating the oötheca and a definite conclusion as to whether or not the Holocompsinae rotate the oötheca must await study of additional material.

Bey-Bienko (1950) erected three subgenera of *Arenivaga;* he believed that the subgenus *Arenivaga* (restricted in distribution to the deserts of the southwestern part of North America and with one species peculiar to the peninsula of Florida) is very close to and is an unquestioned derivative of the subgenus *Psammoblatta,* but is more specialized than the latter. The method of oviposition (i.e., rotation) tends to support Bey-Bienko's conclusion that *A. (Arenivaga)* is more advanced than *A. (Psammoblatta)*. The Polyphagidae need revision, using characters studied by McKittrick (1964). I sent specimens of *Arenivaga (Psammoblatta) cerverae* to McKittrick, and she believes that it is not an *Arenivaga* and does not think it belongs in the Polyphaginae (where she includes *Arenivaga (Arenivaga)* spp.). She wrote (personal communication) that *A.* (*P.*) *cerverae* is close to the Polyphaginae; the female genitalia ". . . are in general arranged like those of *Arenivaga* (*A.*) *bolliana,* and *A.*



Figures 17-24. Oöthecae of Polyphagidae. Fig. 17. *Arenivaga (Psammoblatta) cerverae,* (× 2.0). Fig. 18. *Polyphaga aegyptiaca,* (× 3.6). Fig. 19. Flange of *A. (P.) cerverae,* (× 17.6). Fig. 20. *Euthyrrhapha pacifica,* (× 11.0) (Arrow points to flange which is twisted laterally). Fig. 21. *Arenivaga (Arenivaga)* sp. *A.* (× 6.8). Fig. 22. *Arenivaga (Arenivaga) bolliana.* (× 4.2). Fig. 23. *Arenivaga (Arenivaga)* sp. *B.* (× 4.7). Fig. 24. *Therea petiveriana,* (× 3.4).

(In figures 21-23 the flattened flange is on the right side and in figure 24 it is on the left.)

(*A.*) *apacha,* but are quite different in several particulars. . . . The proventriculus is more like that of *Polyphaga aegyptiaca* than that of *Arenivaga apacha.*" The fact that *A. (Psammoblatta) cerverae* does not rotate its oötheca whereas species of the subgenus *Arenivaga* do, lends support to McKittrick's view that these should be in different subfamilies and probably should be different genera. A detailed study of the oviposition behavior and structure of the oöthecae of polyphagids may have considerable value in the taxonomy of the Polyphagidae and should add considerably to our knowledge of the evolution of the egg case in the Blattaria.

I consider the rotation of the oötheca as it is found in the Blattellidae (Blattellinae, Ectobiinae, and Nyctiborinae) and all of the Blaberidae to be an advanced type, because once rotated, the anterior eggs (those leaving the oviduct last) covered by the oöthecal membrane are in close contact with tissues in the female's vestibulum (Figs. 2,3). This contact was essential for the evolution of ovoviviparity and viviparity, because in species like *Blattella,* the eggs obtain water from the female while the oötheca is carried externally during embryogenesis. I have seen a female of *Chorisia fulvotestacea* Princis carrying a transparent oötheca, with the keel laterad, containing well developed embryos. The oötheca of *Chorisia* is also very similar to *Blattella.*

Shelford (1913) noted that a female of *Temnopteryx abyssinica* Saussure and Zehntner was carrying an oötheca with the keel directed to one side, and the egg case was so transparent that the eyes of the enclosed embryos were visible. This type of oviposition would be similar to that found in *Blattella* and *Chorisia.* Shelford placed *T. abyssinica* in synonymy with *Hemithyrsocera circumcincta* (Reiche and Fairmaire). Rehn (1933) made *Blatta circumcincta* R. and F. the type of the genus *Burchellia.* Princis (1962) placed *Burchellia* in the Ectobiidae (this would probably be the Ectobiinae in McKittrick's (1964) classification). As far as I know none of the Ectobiinae have transparent oöthecae that are carried for the entire embryogenetic period. Princis (personal communication) states that "Whether Shelford was correct in synonymizing *Temnopteryx abyssinica* Sauss. and Zhnt. under *Burchellia circumcincta* (R. and F.) is somewhat doubtful. Although Shelford had examined the type of *abyssinica,* he placed the species under *B. circumcincta* with a query. It seems that Shelford himself was uncertain."

In discussing oviposition by present day oviparous cockroaches, Laurentiaux (1959) stated that the oötheca is generally carried for a month or longer attached to the female before she abandons it. This is not true for most oviparous species which drop their oöthecae within a few days after forming them. Carrying the oötheca during the entire embryogenetic period can be considered to be the most advanced type of oviposition behavior among oviparous Blattaria and is comparatively rare (at present this is known to occur only in *Blattella* and *Chorisia*).

TABLE 1. — DIRECTION OF ROTATION OF OÖTHECAE IN DIFFERENT SPECIES OF POLYPHAGIDAE AND BLATTELLIDAE

Species	Number of Oöthecae Rotated to: Left	Right	Source[a]
Polyphagidae			
Arenivaga (Arenivaga) sp. *A*	0	1	
Arenivaga (Arenivaga) sp. *B*	3	1	
Arenivaga (Arenivaga) bolliana (Saussure)	1	0	McKittrick (1964)[b]
Therea petiveriana (Linnaeus)	3[c]	3[d]	
Blattellidae			
Blattellinae			
Blattella germanica (Linnaeus)	?[h]	usual	Gould and Deay (1938)
	0	?	Blochmann (1887)
	0	?	Ross (1929)
	0	1	Pope (1953)
	few	usual	Willis *et al.* (1958)
	0	49	Wheeler (1889)
	3	97	Wille (1920)
	6[c]	62	
Blattella humbertiana (Saussure)	0	27	
Blattella unicolor (Brunner)	0	20	
Blattella vaga Hebard	few	usual	Willis *et al.* (1958)
Ischnoptera deropeltiformis (Brunner)	2[c]	18	
Ischnoptera panamae Hebard	6[d m]	34	
Ischnoptera rufa rufa (Degeer)	33	78	
Loboptera decipiens (Germar)	0	2	
	0	?	Lefeuvre (1959)
Parcoblatta pensylvanica (Degeer)	3[c]	8[c]	
Parcoblatta uhleriana (Saussure)	0	1	
Parcoblatta virginica Brunner	0	1	McKittrick (1964)[b]
Pseudomops septentrionalis Hebard	1	0	McKittrick (1964)[b]
Shawella couloniana (Saussure)	3[d s]	75	
Symploce hospes (Perkins)	4[c]	111	
Tartaroblatta tartara (Saussure)	0	?	Bey-Bienko (1950)
Tartaroblatta karatavica Bey-Bienko	0	?	Bey-Bienko (1950)
Xestoblatta immaculata Hebard	2[c]	24	
Ectobiinae			
Ectobius pallidus (Olivier)	0	19	Roth and Willis (1957)
Ectobius panzeri Stephens	27	3	Brown (1952)

a) Where no reference is given the observations refer to this study.
b) From a photograph of a female carrying an oötheca
c) Oviposited by one female
d) Oviposited by 2 females
h) ? means that the number observed was not mentioned.
m) One of these females also rotated to the right.
s) These 2 females also rotated to the right.

The possible stages through which rotation evolved in the Blaberoidea, from a polyphagid-like form is given in Fig. 25. The examples shown are not necessarily the ancestral lines. A species in which the oötheca possessed a long flange and was not rotated could have given rise, by reduction of the flange, to a blattellid-like species that did not rotate, or to a polyphagid-like stock that had a primitive type of rotation in which none of the eggs were held within the vestibulum. The polyphagids with primitive rotation could have evolved into advanced rotating individuals, by a complete loss of the flange, thus allowing the anterior eggs in the oötheca to remain in the vestibulum of the female. However, advanced rotation also could have arisen from a non-rotating blattellid whose oötheca lacked a flange and in which the anterior eggs were already housed in the vestibulum. Longer retention of the oötheca led to species like *Blattella* and finally retraction into the uterus occurred with the final evolution of ovoviviparity, and viviparity in the Blaberidae.

Since all of the Blaberidae that have been observed ovipositing are levorotatory (i.e., they rotate the oötheca so the keel faces the left), they probably arose from a *Blattella*-like stock that was levorotatory. Table 1 shows the direction of rotation of different species of Blattellinae. With the exception of *Ectobius panzeri* and *Ischnoptera rufa rufa*, the females of most species observed are dextrorotatory (i.e., they rotate the oötheca so the keel faces the right). Thirty percent of the oöthecae of *Ischnoptera rufa rufa* were rotated to the left (Table 1). Individual oviposition records were kept of 15 females of *I. rufa rufa* (Table 2), and it was found that 4 females were levorotatory, 4 were dextrorotatory, and 7 rotated in either direction. However, females that rotated their oöthecae in both directions usually rotated predominately in one direction only (Table 2, females 5,7,8,10,11).

Because the oöthecae of *Blattella* spp. remain attached to the female during embryogenesis and the eggs gain water from the mother, this genus is considered to be an important link between the oviparous Blattellidae and the ovoviviparous and viviparous Blaberidae (Roth, 1967). However, the 4 species of *Blattella* usually rotate their oöthecae to the right (Table 1), whereas all the internal incubators (Blaberidae) are levorotatory.

Brown (1952) suggested that *Ectobius panzeri* which generally rotates its oötheca to the left (Table 1) probably tends to rotate the egg case towards the side with the most eggs (if there is an odd number of eggs produced). I counted the eggs in 20 oöthecae of *Blattella germanica*, all of which had been rotated to the right; in making the counts the terminal eggs (those laid first and last) were not included since these are placed about on the midline and each lies partly on the left and right sides. Ten of the 20 oöthecae had an even number of eggs on each side. Of the remaining 10 oöthecae, 9 had one more egg on the left side, and 1 had one more egg on the right side. These results contradict Brown's hypothesis and it is likely that the direction of rotation is not influenced by the number of eggs on either side of the oötheca.

Table 2. — Individual oviposition records of females of *Ischnoptera rufa rufa* showing the direction of rotation of their oöthecae.

Female Number	Number of Oöthecae Rotated to: Left	Right
1	6	0
2	4	0
3	2	0
4	2	0
5	4	1
6	3	4
7	2	5
8	2	5
9	2	3
10	1	5
11	1	4
12	0	5
13	0	6
14	0	7
15	0	7

All of the females of *Blattella germanica* in our culture rotate their oöthecae in one direction only, usually to the right. Although I recorded only one left-rotating female in Table 1, I have observed several others and none rotated their oöthecae in both directions. In rare cases the oötheca is carried with the keel dorsad, or the oötheca is incompletely rotated and is only slightly tilted to one side (Wheeler, 1889; Ross, 1929; Willis *et al.*, 1958). It seems logical that the direction of rotation is a genetic character and by inbreeding I have tried to obtain a strain of *Blattella germanica* in which the left rotating females occur more frequently. Initially, I reared 206 female offspring from dextrorotatory mothers. Only one of the offspring rotated to the left and the remaining 205 were dextrorotatory like their mothers. The one left-rotating female oviposited 4 times and all her oöthecae were rotated to the left. The offspring of each of these oöthecae were reared and brothers and sisters were randomly inbred. The results from the females of the four oöthecae were as follows:

	Number of Females Rotating to the:	
Oötheca Number	*Left*	*Right*
1	0	10
2	1	10
3	1	14
4	0	10

The 2 left-rotating females have been inbred with their brothers but the females have not yet matured, as of this writing.

The offspring from several oöthecae of the left-rotating female shown in Table 1, were inbred and the direction of rotation of the resulting females was recorded with the following results (these females were discarded after the eggs in the first oötheca hatched):

	Number of Females Rotating to the:	
Oötheca Number	*Left*	*Right*
1	0	13
2	0	11
3	1	4
5	1	9

The 13 right-rotating females from oötheca number 1 (above) were reared and the F_1 individuals were randomly mated to their brothers. Each female oviposited from 3 to 5 times, producing a total of 57 oöthecae all of which were rotated to the right. The offspring of 12 of the above F_1 females were randomly inbred to their brothers and all of 202 F_2 females that were reared rotated their oöthecae to the right.

The one levorotating female from oötheca number 3 (above) was mated to a brother and their offspring were mated to 2 different males (A and B) that originated from the same oötheca. Four of the five females mated to male A produced 3 to 4 oöthecae each (total of 13), all of which were rotated to the right. One female produced 3 oöthecae all rotated to the left. Unfortunately, this female did not mate and none of the eggs hatched. The six females mated to male B each produced 3 oöthecae (total 18) all of which were rotated to the right. The one left-rotating female from oötheca number 5 (above) has been inbred but the offspring have not yet matured. The offspring of the females mated to brothers A and B were inbred and the results of these crosses were as follows:

Female No.	*Number of Female Offspring Rotating:* Left	Right
Mated to ♂ A		
1	0	15
3	0	35
5	1	24
Mated to ♂ B		
6	0	18
7	1	4
8	0	8
9	0	24
10	0	17
11	2	8

These experiments are still in progress but it is clear that if rotation is a genetic trait it is probably polygenic. Many genes may be involved in determining the direction of rotation of the oötheca and a long period of intensive inbreeding may be required to show this. One difficulty lies in the fact that although one can select levorotatory females for breeding, the males have no comparable visible character to indicate what their genetic makeup is for this trait.

SUMMARY

All cockroaches extrude their eggs with the micropylar ends dorsally oriented and the keel of the oötheca facing upwards. Some species carry the oötheca in this position until depositing it, whereas others rotate the egg case 90° before dropping or retracting it into the uterus. The position in which the oötheca is carried at the time it is deposited is significant taxonomically and also played an important role in the evolution of ovoviviparity and viviparity.

Rotation occurs only in some members of the Blaberoidea (Polyphagidae, Blattellidae, and Blaberidae — the phyletic line in which internal incubation evolved) but not in the Blattoidea (Cryptocercidae and Blattidae — the line in which ovoviviparity did not evolve). Rotation reoriented the oötheca so that the long axes of the eggs lay in the plane of the cockroach's width, a position which allowed for the stretching of the uterus once the egg case was retracted into the female's body. Rotation in the oviparous Blattellidae may be considered to be a preadaptation for the evolution of internal incubation in the Blaberidae.

The type of rotation found in the Polyphagidae is considered to be primitive because none of the eggs are hidden within the vestibulum; the polyphagid oötheca has a flange by which it is held in the

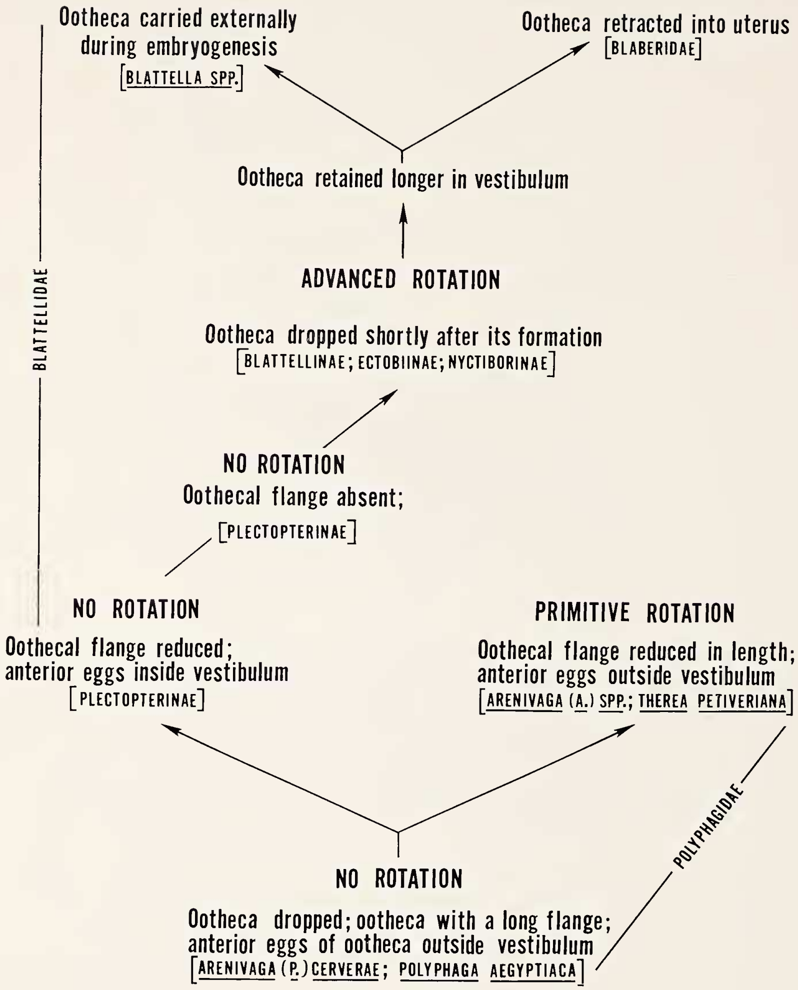


Figure 25. Possible pathways showing how rotation of the oötheca in the Blaberoidea and subsequent retraction of the egg case into a uterus could have evolved from a polyphagid-like ancestor.

female's paraprocts. The rotation exhibited by the Blattellidae (Blattellinae, Ectobiinae, and Nyctiborinae) and all of the Blaberidae is more highly evolved or advanced because once rotated the anterior eggs in the oötheca are in close contact with the tissues in the vestibulum. This contact was essential for the evolution of ovoviviparity and viviparity, because in species like *Blattella,* the eggs, which are carried externally, obtain water from the female.

The evolution of rotation from a polyphagid-like form whose oötheca had a long flange and was not rotated, may have occurred as follows: Reduction of the flange could have resulted in a blattellid-like species that did not rotate its oötheca and a polyphagid-like stock with a primitive rotation. Advanced rotation could have evolved from a non-rotating blattellid whose oötheca had already lost the flange.

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